EIDER, SHELDUCK, AND OTHER PREDATORS, THE MAIN PRODUCERS OF SHELL FRAGMENTS IN THE WADDEN SEA: PALAEOECOLOGICAL IMPLICATIONS

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ABSTRACT. Seventy five per cent by weight of the > 2 mm carbonate fraction of Wadden Sea sediments consists of fragmented shells, thirty per cent > 8 mm and forty five per cent in the 2–8 mm fraction. Eiderducks (*Somateria mollissima*) feed mainly on mussels (*Mytilus edulis*) and cockles (*Cerastoderma edule*). Shells are crushed internally to fragments with a size-range from < 0·1 to 8 mm, twenty per cent were < 1 mm, sixty per cent 2–8 mm. One-third to one-half of the fragments in the 2–8 mm fraction in the sediments are due to eider predation alone. Other birds, crabs and fish probably produce the remaining fragments of this fraction. Shelduck (*Tadorna tadorna*) feed on the small gastropod *Hydrobia ulvae*; a varying amount (seventeen to thirty two per cent by weight) of shells was found intact in their faeces, but the remainder is fragmented. Around forty per cent by weight of *Hydrobia* shells in the Wadden Sea sediments is broken. This can be attributed to shelduck and other predators (e.g. knot) feeding on *Hydrobia*. Fragments in the > 8 mm fraction may also be produced by predators (shore crabs, oystercatchers). Physical destruction plays a minor role in the Wadden Sea. Shell fragmentation cannot be used as a measure of water turbulence. The high percentage of shell fragments indicates high predation pressure. However, the use of shell fragmentation to estimate predation pressure in fossil faunas is not possible, because some predators leave one (oystercatchers) or both valves (*Asterias*) intact. Despite high fragmentation fidelity of the death assemblage to the living fauna of the Wadden Sea is high. Physical destruction would leave only fragments of durable skeletons with low fidelity to the living fauna.

FRAGMENTATION of shells in marine sediments may be due to biological or physical processes. Early workers for example Woodward (1875), Verrill (1882) and Walther (1893, 1910), stressed the importance of shell crushing by predators, mainly crustaceans and fish. Later, more attention was paid to mechanical fragmentation, which was also studied experimentally (Klähn 1932; Chave 1960; Force 1969). Van Straaten (1952, 1956) introduced a 'crush factor' (the percentage of broken shells of the entire shell material of one species) to be used as an indicator of the degree of wear of the shell material during transport, a method also advocated by Ager (1964, p. 199). A comparable correlation between fragmented shells and water turbulence has been suggested by Vokes (1948), Bissell and Chilingar (1967), and Link (1967). Studies of experimental abrasion and fragmentation of skeletal elements are still popular, for example, Kidwell and Baumiller (1990), Kotler *et al.* (1992).

Biological factors in shell fragmentation have been stressed by Ginsburg (1957), Schäfer (1962) and Trewin and Welsh (1976). Carter (1968) and Vermeij (1978, 1987) summarized an extensive literature dealing with shell fracturing by molluscan predators. The dual nature of shell fragmentation is now well accepted (Chave 1964; Pilkey 1964, 1969; Swinchatt 1965; Cadée 1968; Palmer 1977; Dodd and Stanton 1981), but it makes interpretation of fragmented shells difficult. Although Dodd and Stanton (1981) suggested that the products from these two processes are recognizable, Powell *et al.* (1989) more realistically remarked that the interpretation of the fragmented portion of a molluscan death assemblage is often difficult. Parsons and Brett's (1991) statement that 'fragmentation is clearly a measure of environmental energy, with the exception of biologically mediated breakage' gives little hope for solving the problem. Their suggestion that

[Palaeontology, Vol. 37, Part 1, 1994, pp. 181–202, 1 pl.]
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environmental energy is the main cause of shell fracturing is counter to that of Cadée (1968) and Dodd and Stanton (1981), who suggested biological factors such as predation are most important in shell breakage. Only in a few cases can shell fracturing be attributed mainly to physical destruction in the surf zone of a sandy (Hollmann 1968) or a pebbly (Trewin and Welsh 1972) beach.

Shell fragments produced by predators are sometimes very predator specific (Vermeij 1978, 1987), but later abrasion and activity of boring organisms may make these fragments similar to those produced by physical processes (Schäfer 1962). Quantitative separation of biological and physical processes in fragmentation therefore does not seem possible. Fracturing by water energy will be largely caused by waves and breakers and is thus confined to the coastal zone, but in this coastal zone predators (mainly birds) are also active (this paper). Shell fragments may be produced sublitorally by predators (fish, crustaceans, birds) and transported as fragments to the coast. Sublittoral currents may not be strong enough to fragment shells (Schäfer 1962; Feige and Fürsich 1991). Flemming *et al.* (1992) stated that normal tidal currents are not strong enough even to transport shells in the Wadden Sea: subtidal shell beds are formed there by a largely passive gravitational transport in the wake of channel migration.

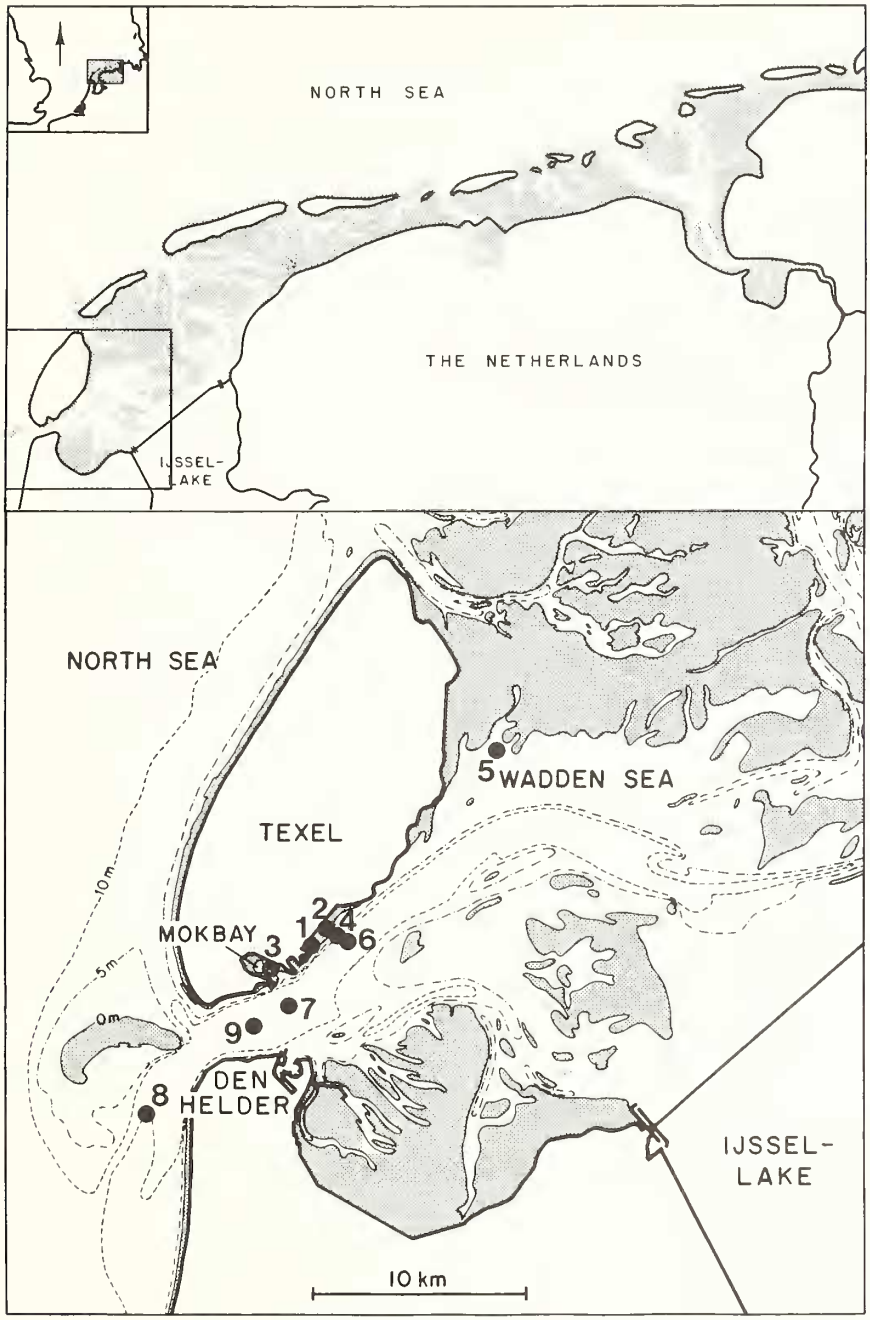
With the increasing quantitative knowledge of food webs in the recent marine environment, it now becomes possible to estimate the amount of the total biomass of molluscs broken by different predators for some areas. This can be compared with the actual 'crush factor' found for the empty shells in the sediment and may enable an estimation of the importance of biological versus physical shell fragmentation. Eisma and Hooft (1967) were the first to apply this method. They compared the amount of shell fragments present in Recent Dutch open-sea coastal North Sea sediments and concluded that 50 to 100 per cent of the fragments were due to flatfish (plaice) predation. For the Holocene Dutch open-sea, coastal sediments they estimated that at least 10 per cent, but probably much more of the molluscan fragments were due to plaice predation. An admixture of fragments from Eemian sediments, breakage by other predators, and some physical fragmentation in the surf zone could account for additional fragmentation. Similar quantitative work has not been carried out since.

In this paper I concentrate on the Dutch Wadden Sea. In the last three decades a large amount of data has been collected on macrobenthos biomass and production in this area (Beukema 1976, 1982*b*, 1989; Dekker 1989; Dankers *et al.* 1989) and on predators, mainly birds, compiled by Hulscher (1975), Swennen (1975) and Smit (1981).

Data are presented on shell fracturing in the Dutch Wadden Sea by two duck species, shelduck (*Tadorna tadorna*) and eider (*Somateria mollissima*). Both species ingest whole molluscs and crush the shells in their gizzard, so that they can digest the meat. Shelduck feed on small molluscs, such as *Hydrobia ulvae*, and small worms and crustaceans (compilation in Bauer and Glutz 1968), 'sieving' those > 2 mm from the sediment with their beak (Thompson 1982). They use different methods, depending on water depth, to collect food (Bryant and Leng, 1975, fig. 4), and leave characteristic feeding traces on the sediment (Cadée 1990), but do not dive. Eider feed mainly on larger molluscs like the cockle (*Cerastoderma edule*) and mussel (*Mytilus edulis*) (see Swennen 1967), which are collected by diving. These data are compared with available data on production of these molluscs (Dekker 1979; Beukema 1980, 1982*a*; Dankers *et al.* 1989) to estimate the fraction broken. This is compared with the actual percentage of broken shells of the same species in Wadden Sea sediments. From this comparison it is possible to estimate the role of these ducks in the production of shell fragments in Wadden Sea sediments.

MATERIAL AND METHODS

Faeces of eider were collected from several locations on the dike along the southern part of Texel (Text-fig. 1), where a small part of the eider population roosts (most eider 'roost' on open water, Swennen 1976, 1991). Such faeces usually consist of the undigestible parts of one food item only, such as mussels and cockles, and when these are scarce, shore crabs (*Carcinus maenas*), or periwinkles (*Littorina littorea*) (Cadée 1991). To get rid of the organic coating of the faeces they



TEXT-FIG. 1. Location of sampling stations (mostly in 1992), numbering according to depth (from station 1, High Water line, to 20 m depth for station 9).

were shaken with water in glass beakers, and the water decanted. This was repeated several times until the decanted water became more or less clear. Part of the smaller particles in the faeces, roughly $< 50\ \mu m$, were inevitably also removed during cleaning. The size distribution of the shell

fragments was measured by dry sieving over a series of sieves with mesh sizes ranging from 0·1 to 8 mm.

Faeces of shelduck were collected on the tidal flat in the Mokbay (Text-fig. 1) where shelduck were observed feeding. Their faeces are easy to recognize by their size, and they are often full of hydrobiids. These faeces were treated in the same way as the eider faeces, but because shelduck faeces also contain varying amounts of larger sand and shell grains picked up during feeding, the size frequency distribution of *Hydrobia* fragments could not be measured by sieving. Some faecal counts were made of the number of broken (only top fragments were counted) and entire Hydrobia shells. The crush factor (weight of all *Hydrobia* fragments as a percentage of total weight of *Hydrobia* shells) was also determined.

Bottom samples were collected at a number of locations near Texel (Text-fig. 1). A Van Veen grab was used for sublittoral sites and intertidal sites were collected by hand. They were sieved over 1, 2 and 8 mm sieves and a 'crush factor', i.e. the weight percentage of broken shells of the total amount (Van Straaten 1956), was measured from 1000–2000 particles in the > 2 mm fraction. Also crush factors for the dominant species such as cockle and mussel were measured separately. For the small *Hydrobia* the fraction 1–2 mm also was used to estimate this crush factor.

Eider faeces

Fortunately an individual eider usually feeds on one food item at a time. Its faeces therefore contain only material of one food species. In the faeces studied, all mussels and cockles were crushed. In faeces of eider feeding only on *Littorina*, a few intact shells were observed. The shell fragments produced were angular and sharp edged (Pl. 1). The size–frequency distributions of fragments in faeces from the Wadden Sea were similar for the three different types of food: *Mytilus*, *Cerastoderma* and *Littorina* (Text-fig. 2). The bulk of the fragments was in the fraction 2–4 mm; very few fragments were larger than 8 mm, approximately 20 per cent was smaller than 1 mm, and 60 per cent was in the 2–8 mm range. Eider faeces collected in the Baltic at Åland, where they were feeding on smaller (up to 30 mm in length) and thin-shelled *Mytilus*, had a different size frequency distribution (Text-fig. 3). Fragments had a peak in the 1–2 mm fraction, 60 per cent were 1 mm, and only 6 per cent > 2 mm.

Shelduck faeces

Shelduck faeces consisted mainly of *Hydrobia* shells. Remains of additional prey items were of small bivalves, *Macoma balthica*, *Cerastoderma edule* and *Abra tenuis*, and varying amounts of worms and crustaceans. The remainder consisted of coarse sand grains and a few fragments of large bivalves picked up by shelducks during feeding. These grains might help in grinding *Hydrobia* shells. However, not all *Hydrobia* shells appeared to be broken. In fact, a whole range from small fragments to entire shells could be found (Text-fig. 4). A number of *Hydrobia* were even still alive after passage through the shelduck, which takes one to two hours. This was not reported earlier and is a possible factor in short-distance dispersal of this gastropod (Cadée 1989). A comparable survival of 10 per cent of gastropods consumed in the intertidal of the Pacific by the fish *Asemichthys taylori* was reported by Norton (1988). Apparently an intact shell plus its operculum are a sufficient barrier against digestion. Droppings (all the faeces produced at one moment) contain remains of a few hundred to over a thousand *Hydrobia* shells (Table 1). Crush factors for *Hydrobia* shells in the

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EXPLANATION OF PLATE 1

Different fractions of shell fragments from eider faeces collected on Texel. Rows from top to bottom are 4–8 mm, 1–2 mm, 0·5–0·7 mm and 0·1–0·2 mm fractions, respectively. Left column (figs 1–4): *Mytilus edulis*, 25 January 1988. Right column (figs 5–8): *Cerastoderma edule*, 14 May 1991. All figures ×2.

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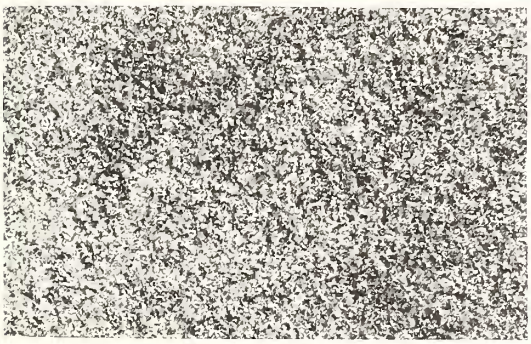

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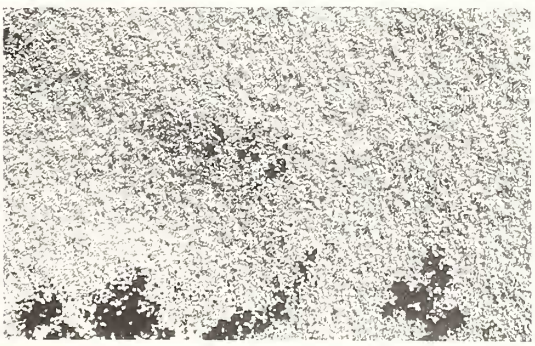

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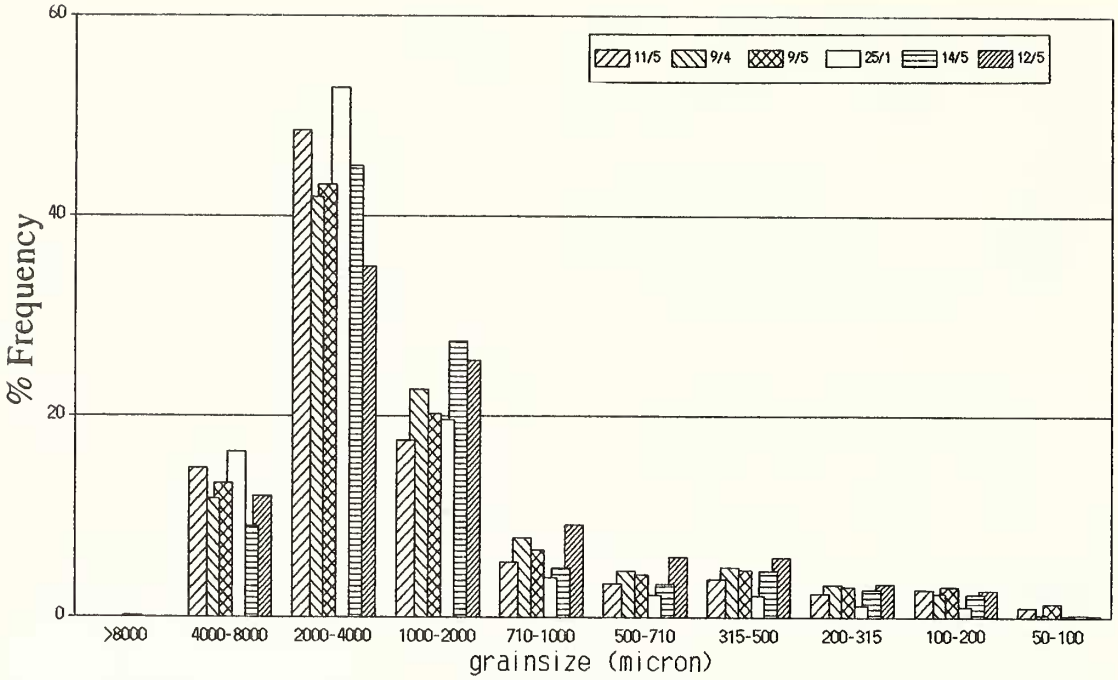


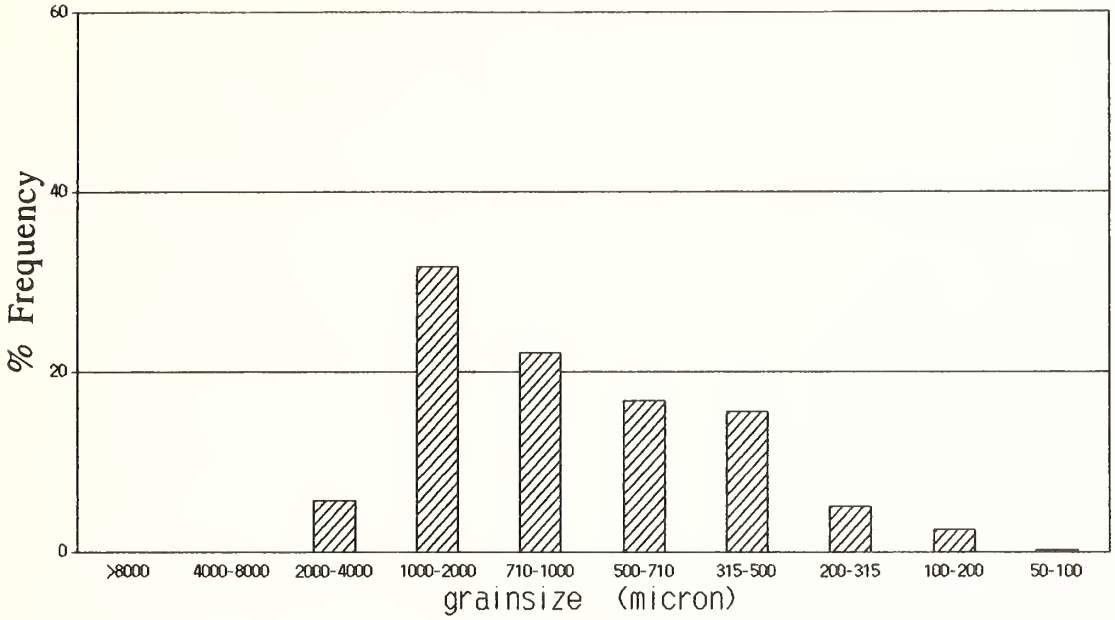
TEXT-FIG. 2. Size frequency distribution of shell fragments in eider faeces collected on the dike of Texel. Numbers in legend indicate date (month/day) in 1991 (except 1988 for 25/1). Faeces comprised *Mytilus* (9/5 and 25/1), *Cerastoderma* (11/5 and 14/5), and *Littorina* (9/4 and 12/5) fragments.

faeces vary from 68 to 83 per cent (Table 1). Faeces in which high amounts of soft food items were observed, mainly polychaetes, had lowest crush factors.

WADDEN SEA BOTTOM SAMPLES

In most cases all the sand grains passed the 1 mm sieve leaving only shells and a variable amount of peat fragments on the sieve. The shell carbonate fraction > 2 mm accounted on average for 95 per cent (range 90·1–99·3 per cent) of bivalves. Gastropods (mainly *Littorina littorea*) formed only 3 per cent (range 0·3–4·6 per cent), the rest – 2 per cent (0·1–5·3 per cent) – consisted largely of barnacle fragments (Text-fig. 5). On average 2·7 per cent of the fragments, all belonging to bivalves, could not be identified to the species level. Species composition (Text-fig. 6) indicates that *Cerastoderma edule* and *Mytilus edulis* are the main component (respectively 44·7 and 35·7 per cent) of the fraction > 2 mm. The small *Hydrobia* was a minor component of the > 2 mm fraction.

The deepest stations (stations 7–9, Text-fig. 1), near the inlet, contained on average 19·6 per cent *Spisula* sp., mainly *S. subtruncata*, a North Sea species occurring in dense patches offshore (Eisma 1966; Offringa 1991). Only occasionally this species settles in the Wadden Sea and may survive during mild winters, but dies in periods of ice formation on the tidal flats (Cadée and Hegeman 1975). High percentages of *Spisula* shells in Wadden Sea sediments indicate North Sea influences (as mentioned already by Krause 1950). Stations 7 and 9 (Text-fig. 1), moreover, contained the gastropod *Bittium reticulatum*, which is a fossil of Eemian age in The Netherlands (Van Regteren Altena 1937; Van Regteren Altena *et al.* 1955). This indicates that Eemian deposits are eroded in the deep inlet area. Indeed Eemian deposits were found exposed in the deepest inlet channels below *c.* 20 m depth by Sha (1989). Therefore some of the other shells, including *Cerastoderma* and *Mytilus*, which were also abundant in the Eemian (Spaink 1965), may be of Eemian age. For a



TEXT-FIG. 3. Size frequency distribution of *Mytilus* fragments in eider faeces from Åland, Baltic Sea, in 1991.

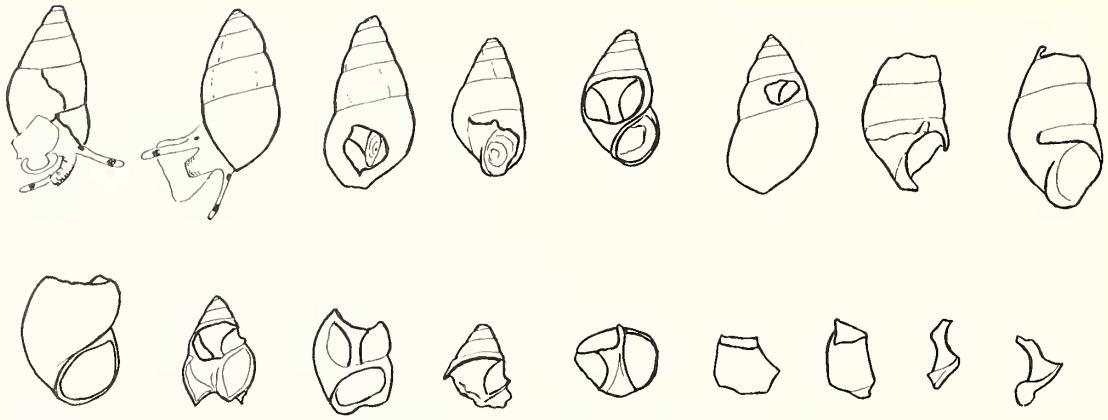
comparison of shell fragments in bottom deposits and the feeding activity of eider and shelduck in the Wadden Sea, I will only consider to stations 1–6 (Text-fig. 1) in the Wadden Sea proper, where there is less admixture of North Sea and fossil shells.

Crush factors in all bottom samples were high: around 70 per cent for all species together (Text-fig. 5). Crush factors were highest in the intertidal and shallow Wadden Sea stations (1–3, Text-fig. 1) decreasing with depth in the gully stations (4–6, Text-fig. 1), and still lower in the stations in the deeper inlet and just outside (stations 7–9). Near the High Water line (station 1) sorting occurs due to wave action (Van Straaten 1954, p. 21). The coarse samples had a higher content of entire shells than the samples with mainly finer material. Four separate samples therefore were taken here to cover this range and the results were pooled: the average crush factor for this pooled sample (station 1) is comparable to that of the other shallow stations (stations 2–3).

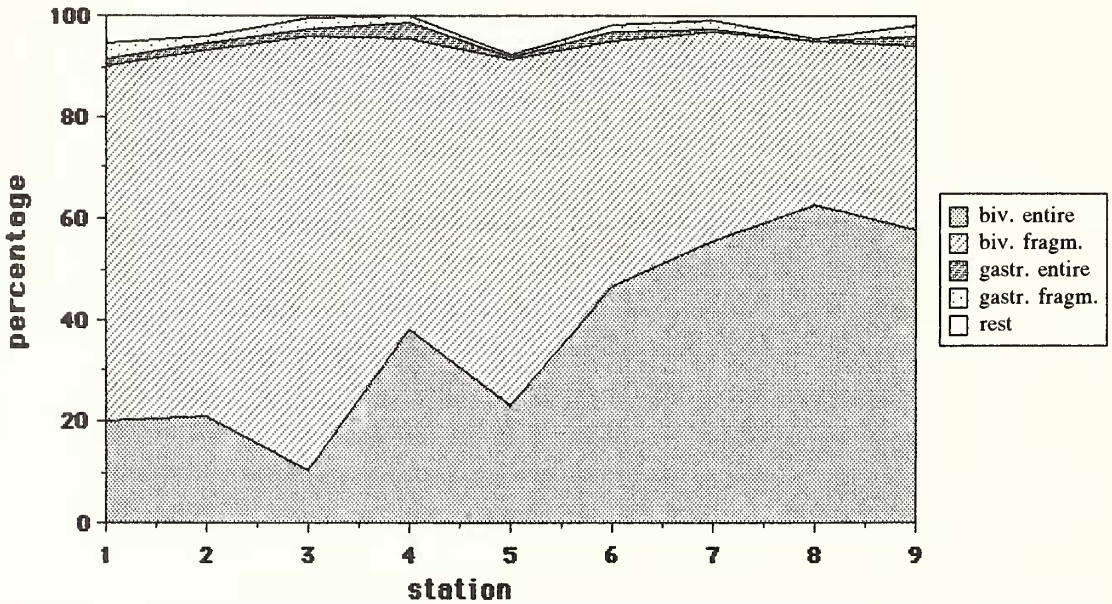
Crush factors varied between species (Text-fig. 7). They were high for typical Wadden Sea molluscs such as *Mytilus*, *Cerastoderma* and *Littorina*, and lower for the North Sea bivalve *Spisula* sp. Typical Wadden Sea species also have relatively high crush factors in samples outside the Wadden Sea.

HYDROBIA PRODUCTION AND ITS CONSUMPTION BY SHELDUCK

The average number of shelduck occurring in the Dutch Wadden Sea is 21 000 (Smit 1981). Annual consumption by shelduck in the Dutch Wadden Sea is estimated at $7{\cdot}1 \times 10^8$ g ash-free dry weight (afdw), being 7 per cent of the consumption of all carnivorous birds (Smit 1981). As shelduck feed only on tidal flats (120000 ha for the Dutch Wadden Sea) and not in deeper water, their annual consumption per m^2 tidal flat was estimated at 0·59 g afdw (Smit 1981). Dekker (1979) measured in 1978 an annual production for *Hydrobia* of 2·0 g afdw on the Balgzand, a tidal flat area in the western Dutch Wadden Sea, and higher values of 35·5 g afdw in the Mokbay. However, for the whole western Dutch Wadden Sea this value is probably lower (*c.* 0·6 g afdw m^{-2} tidal flat, Beukema 1981). Year to year variation is large, Balgzand biomass in 1981/1983 amounted to 0·8 g afdw m^{-2} (Dekker 1989) and using a Production/Biomass (P/B) ratio of 0·7 (Dekker 1979) this gives an annual production of only 0·56 g afdw m^{-2} as compared with 2·0 in 1978.

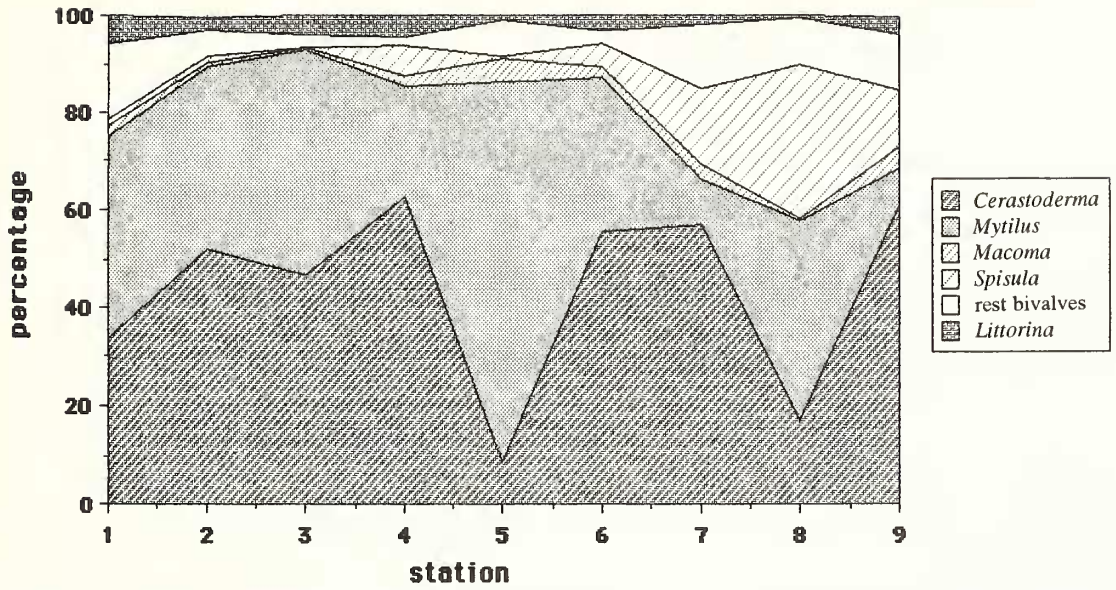


TEXT-FIG. 4. *Hydrobia ulvae* from shelduck faeces ranging from living specimens to small fragments. The largest shell is 4 mm in length.

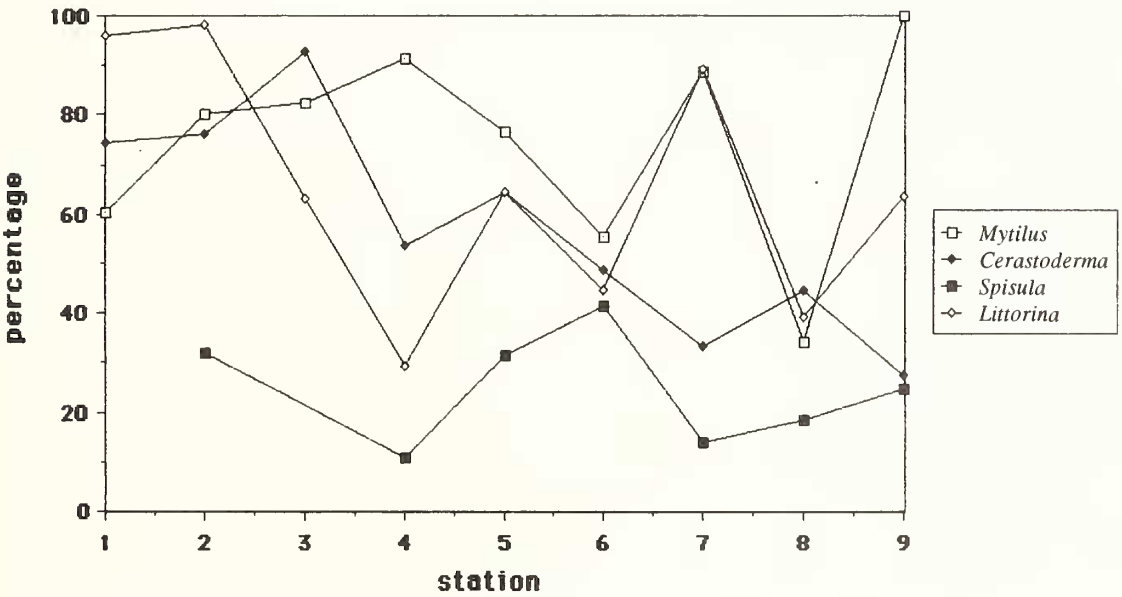


TEXT-FIG. 5. Composition of > 2 mm fraction of Wadden Sea bottom samples; stations arranged according to depth from High Water (1) to 20 m depth (9). Percentages all by weight.

If shelduck were feeding only on *Hydrobia*, they could consume the average annual intertidal production of 0·6 g afdw m^{-2} of this species. They fed for a large part on *Hydrobia* as could be judged from the faeces I collected in Mok Bay, but also took additional prey items (this paper; see also Bauer and Glutz 1968). Assuming that their diet consists for 50 per cent of *Hydrobia* and taking into account that on average 75 per cent of the *Hydrobia* shells are broken inside shelducks (Table 1) we can estimate that 37·5 per cent of the shells of the intertidal *Hydrobia* population are broken by shelduck. This is near the figure for the crush factor for *Hydrobia* observed in intertidal Wadden Sea sediment samples (stations 0–3, average 43 per cent; Table 2). Taking into account that other birds also consume and crush *Hydrobia*, e.g. knots (*Calidris canutus*) (Piersma *et al.* 1994; Dekinga and Piersma 1993), I arrive at an even higher potential crush factor than was



TEXT-FIG. 6. Species composition of the molluscan fraction (> 2 mm) of the same bottom samples as Text-figure 5.



TEXT-FIG. 7. Crush factor (weight percentage of fragments) for four species.

observed. This might indicate that the production estimates for *Hydrobia* are too low. Certainly, production of *Hydrobia* shows large variations from place to place and from year to year. Moreover, *Hydrobia* migrates (Dekker 1979) making estimation of its production difficult.

Dekker (1989) observed higher *Hydrobia* numbers and biomass in the subtidal parts of the western Wadden Sea, on average 4·9 g afdw m^{-2}. Using again his P/B ratio of 0·7 I arrive at a

TABLE 1. Crush factors for *Hydrobia* shells in Shelduck faeces from Mokbay expressed as percentage weight fragments of total weight of *Hydrobia* shells and as percentage number of top fragments of entire shells plus top fragments.

Date	Entire shells (number)	Entire shells (g)	Top fragm. (number)	Top fragm. (g)	Crush factor by weight	Crush factor by number
19 May 1988	277	1·162	875	2·512	68·4	76·0
8 June 1988	77	0·294	530	0·941	76·2	87·3
30 June 1988	25	0·055	560	0·262	82·8	95·7
7 Nov. 1988	52	0·167	135	0·390	70·0	72·2

TABLE 2. Crush factor for *Hydrobia* shells in Wadden Sea sediment samples (weight of shell fragments as percentage of weight of all shells in fraction 1–2 mm + > 2 mm). Station 0: additional samples of drift consisting only of *Hydrobia* shells, Wadden Sea coast, Texel.

Station no.	Total weight (g)	Weight of fragments (g)	Crush factor
0	1·666	0·781	46·9
1	1·113	0·486	43·7
2	1·187	0·486	40·9
3	0·270	0·111	41·1
4	0·676	0·160	23·7
5	0·907	0·162	17·8
6	0·463	0·103	22·3
7	0·822	0·267	32·5

production of 3·4 g afdw m^{-2} for the subtidal areas which comprise *c.* 50 per cent of the Wadden Sea and where shelduck do not feed. Subtidal predation on *Hydrobia* has not been quantified. Potential subtidal predators that crush *Hydrobia* shells are shore crabs, shrimps, flatfish and gobies. But predation pressure by these predators is apparently less here accounting for a relatively low crush factor of *Hydrobia* shells in subtidal sediment samples (stations 4–7, average 24 per cent, Table 2).

I conclude that no physical factor in shell fracturing is necessary to account for the broken *Hydrobia* shells in intertidal Wadden Sea sediments; this probably also holds for subtidal sediments.

COCKLE AND MUSSEL PRODUCTION AND EIDER CONSUMPTION

Swennen (1976) estimated the average number of eider in the Dutch Wadden Sea at 63000. Numbers vary seasonally and consist of a breeding population of about 6000 pairs plus a higher number of non-breeding summer visitors, to a maximum of almost 170000 in winter, mainly due to immigration from the Baltic population. In the Dutch Wadden Sea the food of the eider consists of 40 per cent mussels, 40 per cent cockles and 20 per cent other prey (Swennen 1976) and annual consumption for the Dutch Wadden Sea amounts to *c.*1·2 g afdw m^{-2} or $3{\cdot}2 \times 10^6$ kg for the entire Dutch Wadden Sea of 2600 km^2 (Swennen 1976, 1991). Annual cockle and mussel consumption by eider each amounts to $0{\cdot}4 \times 3{\cdot}2 \times 10^6$ kg afdw = $1{\cdot}28 \times 10^6$ kg. For cockles eaten by eider, shell carbonate weight is *c.* twenty times the ash-free dry weight of the meat (Swennen 1976); this gives an annual deposition of cockle carbonate of $25{\cdot}6 \times 10^6$ kg in the form of shell fragments.

Cockle production varies due to large year to year variations in the cockle population; only few years produce strong enough settlements leading to strong year-classes that in turn form the bulk of the cockle biomass (Beukema 1976, 1982*a*, *b*). Average annual shell carbonate production was estimated by Beukema (1982) at 156×10^6 kg for the intertidal and *c*.10 per cent of this amount for the subtidal Wadden Sea. Eiderducks fragment therefore on average *c*.15 per cent of the cockle carbonate production.

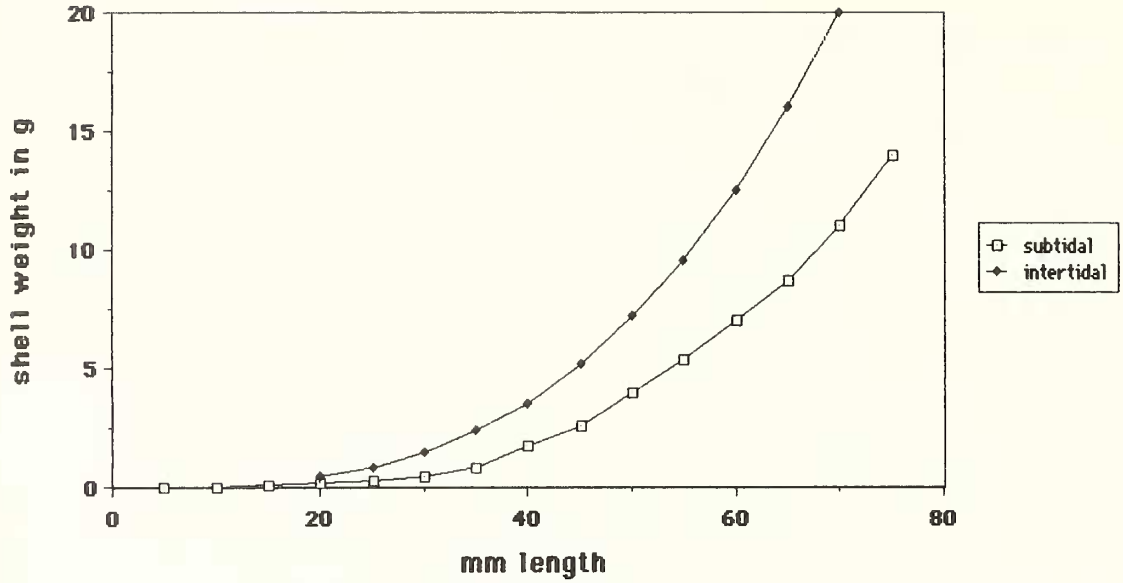
For mussels, data are only available for the annual average biomass present in the western Wadden Sea ($14{\cdot}7 \times 10^6$ kg afdw, Dankers *et al.* 1989). As no data are available on production, I will assume a Production/Biomass (P/B) ratio of one, also used by Beukema (1981) for adult mussels. This value probably holds for subtidal mussels, but P/B is lower in intertidal areas decreasing from one in juveniles to one-tenth in ten-year-old mussels (Thompson 1984; and compilation of Wadden Sea data in Egerrup and Hoegh Laursen 1992). The shell weight to biomass ratio also varies considerably seasonally (Dankers *et al.* 1989), as well as from tidal to subtidal (Baird and Drinnan 1957), making mussel carbonate production more difficult to estimate. The bulk of the mussel population occurs subtidally (Dekker 1989), partly due to mussel culture. For my estimates I have assumed a biomass (ash-free dry weight) to carbonate ratio of six, based on the average biomass/length ratio (N. Dankers pers. comm.) and shell weight/length relation measured for subtidal mussels (Text-figs 8–9). Annual carbonate production by mussels can then be estimated at $6 \times 14{\cdot}7 \times 10^6$ kg. In the western Wadden Sea the average eider population is 48 400 (Swennen 1991). Mussel consumption in this part of the Wadden Sea can therefore be estimated at 48 400/63 000 of the total consumption of $1{\cdot}28 \times 10^6$ kg, and this has to be multiplied by six to arrive at 'consumption' of mussel carbonate, giving $5{\cdot}9 \times 10^6$ kg. This equals 15 per cent of the average annual mussel carbonate production: the same percentage as found for the cockle.

Eiderducks rarely produce shell fragments larger than 8 mm (see Text-fig. 2). They cannot be responsible for the fragments > 8 mm in bottom samples. In the Wadden Sea bottom samples only fragments less than 2 mm were examined. To compare shell fragment production by eiderducks with those present in the bottom samples we therefore have to use fragments present in the 2–8 mm fraction of our bottom samples and keep in mind that 60 per cent of the fragments in eider faeces are in this 2–8 mm fraction. Therefore, the eider reduces 10 per cent of the annual mussel and cockle carbonate production to fragments between 2 and 8 mm in size.

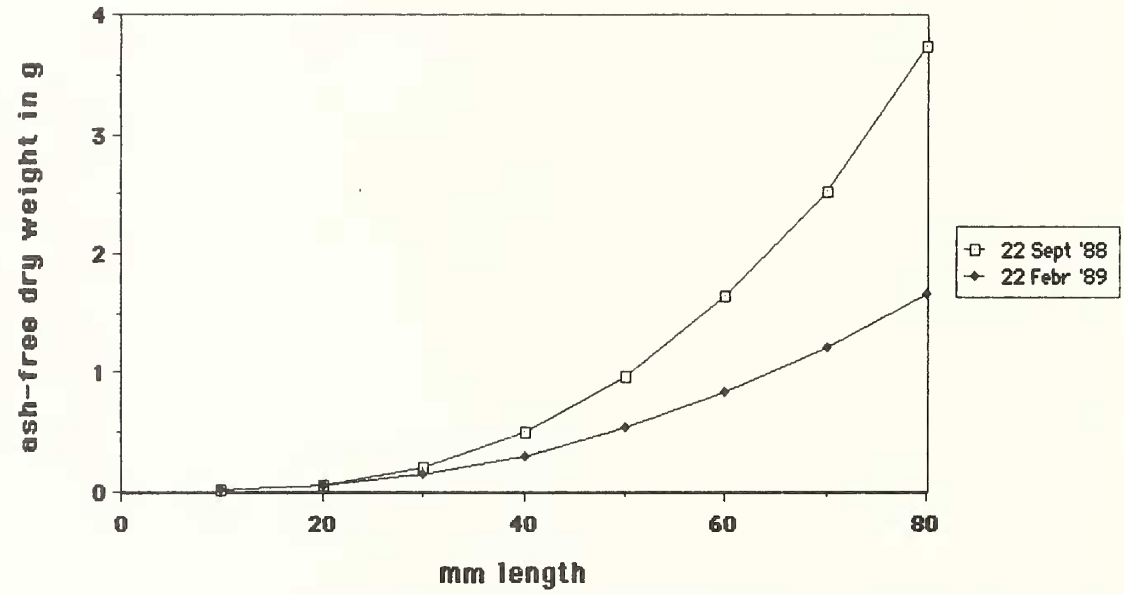
In the bottom samples on average 25 per cent of all the shells are whole, 30 per cent are fragments in the 2–8 mm fraction and 45 per cent are fragments larger than 8 mm (Text-fig. 10). For the cockle and mussel (Text-figs 11–12) respectively 30·4 and 27·9 per cent were found as fragments in the 2–8 mm fraction. This indicates that eider alone could be responsible for *c*.one-third of the fragments in this fraction. If we leave out station 3 in the Mokbay, where a relatively high percentage of fragments was found in the 2–8 mm fraction we can estimate eider contribution at *c*.one-half of the 2–8 mm fragments present in bottom samples. However, the fragments in the Mokbay sample (Text-fig. 13) are very similar to those found in eider faeces (compare with Plate 1, figures 1 and 5). As eider roost (and thus also defecate) in flocks on the water, contribution of eider faeces is not random over the Wadden Sea. This will lead to variation in eider-produced fragments in bottom samples. The number of six stations may, however, be too small to estimate accurately the average 2–8 mm fraction of fragments.

OTHER PREDATORS

The large number of fragments larger than 8 mm in the bottom samples, 45 per cent for all molluscs, 38·9 and 45·2 per cent for cockle and mussel respectively (Text-figs 11–12), must be due to factors other than eider or shelduck predation, Physical factors cannot be ruled out completely. The fact that the highest number of fragments were found in the intertidal stations (stations 1–3; Text-figs 10–12) suggests wave energy. However, some other predators are also known to produce large fragments. Oystercatchers feed, like eider, on cockle and mussel in the Wadden Sea (Smit 1981). They produce characteristic shell fragments, where a small fragment is broken off from one valve

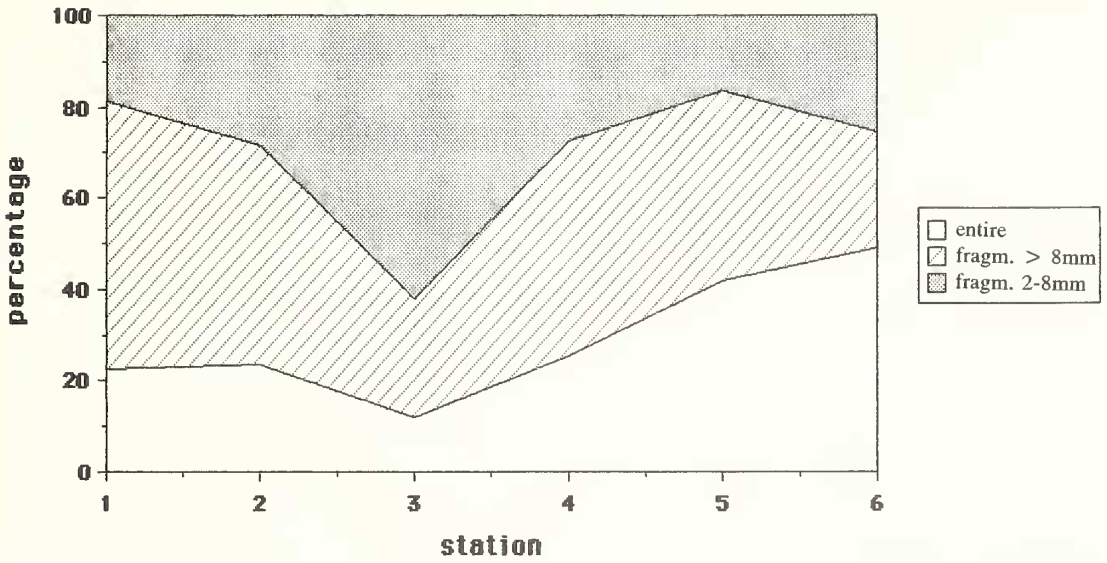


TEXT-FIG. 8. Shell weight (articulated valves) versus shell length for intertidal and subtidal *Mytilus*, based on sixty measurements each; only curves given ($r = 0{\cdot}98$).

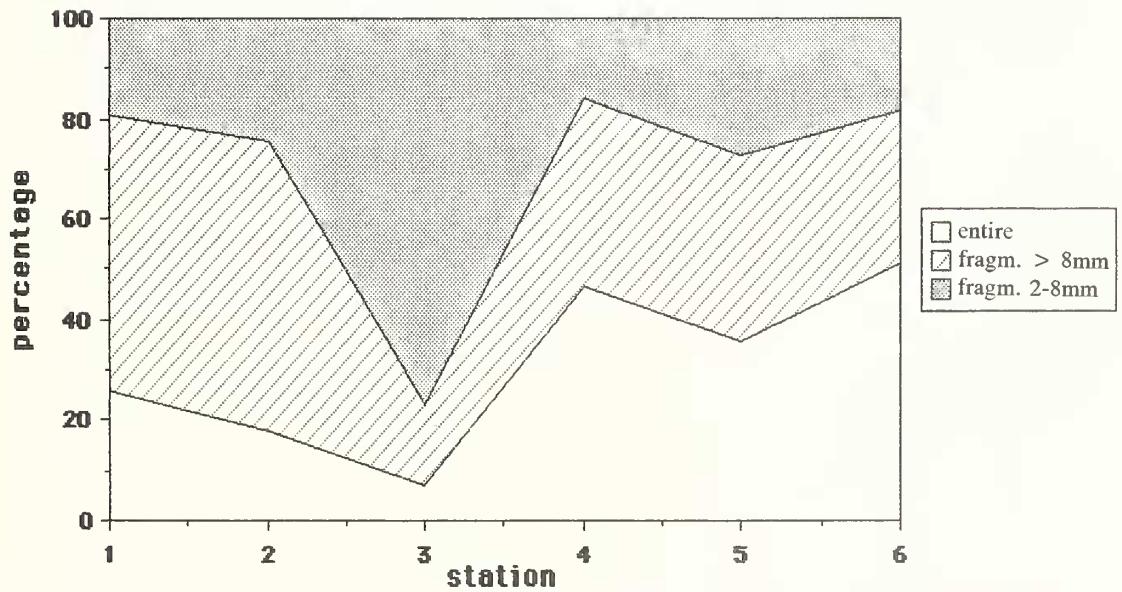


TEXT-FIG. 9. Shell length versus ash-free dry weight for subtidal *Mytilus*, for September and February, indicating loss of biomass during winter; data obtained from N. Dankers.

only, to enable the bird to sever the adductor muscle (Drinnan 1957, 1958; Hulscher 1964; Tinbergen and Norton-Griffiths 1964; Tinbergen 1976). The oystercatcher does not always break a shell, as the bird may succeed in inserting its bill between the valves without damaging them. Oystercatchers consume almost as many bivalves as the eiderducks in the Wadden Sea (Smit 1981).



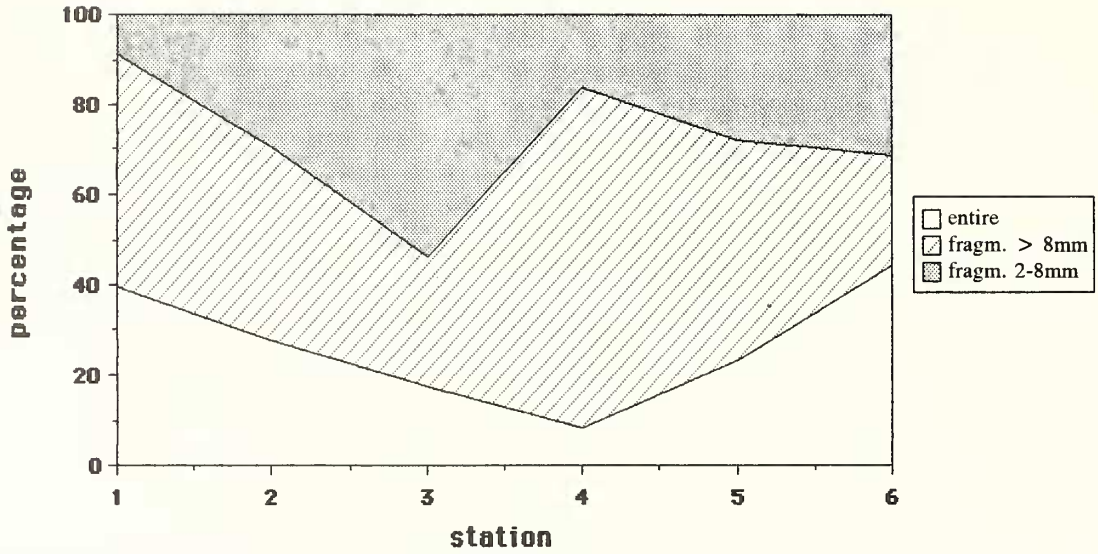
TEXT-FIG. 10. Distribution of entire mollusc shells, fragments > 8 mm, and fragments from 2–8 mm, in the > 2 mm fraction of the Wadden Sea bottom samples.



TEXT-FIG. 11. Distribution of entire *Cerastoderma* shells, fragments > 8 mm, and fragments from 2–8 mm, in the > 2 mm fraction of the Wadden Sea bottom samples.

From Drinnan (1957, 1958) we can estimate that at least 50 per cent of the valves of cockle and mussel consumed remain intact. Hulscher (1981, 1984) found that oystercatchers feeding on *Macoma balthica* left 60–65 per cent of the valves intact.

Another, probably underestimated, predator in the Wadden Sea is the shore crab (*Carcinus*



TEXT-FIG. 12. Distribution of entire *Mytilus* shells, fragments > 8 mm, and fragments from 2–8 mm, in the > 2 mm fraction of the Wadden Sea bottom samples.

TEXT-FIG. 13. Greater than 2 mm fraction of bottom sample from Station 3, strongly suggesting all fragments were produced by eider (compare with Plate 1); ×2.

maenas). Its omnivorous character is well known; its diet includes bivalves (MacPhail 1955; Ropes 1968; Walne and Dean 1972; LeRoux *et al.* 1990). Juvenile crabs feeding on the tidal flats have been best studied (Klein Breteler 1976). Their annual consumption is comparable to that of all five species of bird in the Wadden Sea (Swennen 1975). Subtidal feeding of adults on the mussel culture areas is less well known. Biologists studying the food of this crab have never reported on the fragments produced, but MacPhail (1955) stated that this crab feeds as a rule on shells as large as the width of its carapace. Initial studies on shell fragmentation by shore crabs indicate that identical fragments occur in bottom sediment samples. Finally, shell smashing by herring gulls (*Larus argentatus*) produces large fragments (see Cadée 1989 and references therein), partly by the dropping of shells on (artificial) hard substrates along the Wadden Sea, but also by dropping them on the tidal flat.

One-third to one-half of the fragments in the 2–8 mm fraction can be due to eider predation alone. Herring gulls feeding on molluscs produce, in coughballs and faeces, fragments comparable in size to those in eider faeces (Schäfer 1962; Cadée, unpublished). They are probably as important as eider in crushing shells in the Wadden Sea (Cadée, unpublished). Smaller bivalves have numerous other predators in the Wadden Sea: waders, shore crabs, flatfish and shrimps (Reise 1985, fig. 10.4). This together suggests that most shell fragments in the 2–8 mm fraction are produced by predators.

Entire shells, 25 per cent by weight of the shells in the bottom samples, indicate other causes of death (see below) or predators that leave the shell intact. This holds for the starfish *Asterias rubens*, which is known as a pest on mussel culture areas, but little quantitative data are available on this predator in the Wadden Sea. A number of authors have indicated its role as a predator in soft-bottom communities in NW Europe (Anger *et al.* 1977; Nauen 1978; Allen 1983). In Kiel Bay *Asterias* consumes daily almost 3 per cent of the macrobenthos (including bivalves) according to Nauen (1978). All sizes of mussels up to the largest (80 mm length) may be consumed by *Asterias*. Only specimens with a large adductor muscle may escape *Asterias* predation (Hancock 1965). Finally human influence has to be mentioned. On average about 5 per cent of the adult cockle population is fished annually, but in years with low cockle biomass a higher percentage is fished. These cockles are cooked at sea, and their empty shells dumped in the Wadden Sea. Mussel fishery removes shells from the Wadden Sea.

Oystercatchers have already been mentioned which leave > 50 per cent of the valves of bivalves actually eaten, intact. Cockle mortality in the Wadden Sea, leaving valves intact, may also result from other factors like parasites, severe winters (Kristensen 1957, 1959), or low oxygen content (Cadée 1991). Burial of mussels under a layer of storm-deposited sand may also cause mortality (Kuenen 1942; Theissen 1968). According to Kuenen (1942) mussels covered by more than 20 mm of sand will die. Mussels may also die in subtidal culture areas when seeded in too thick layers (N. Dankers pers. comm.).

The large amounts of shells fragmented by predators in the Wadden Sea probably explained most of the shell fragments found in the Wadden Sea bottom samples. The role of other predators has yet to be quantified in the same way as done here for eider and shelduck to give a more quantitative estimate. This awaits the results of further studies now in progress. The high percentage of shell fragments in Wadden Sea sediments indicates a high predation pressure. However, we have to take into account the fact that not all predators crush shells. Moreover, LaBarbera (1981) and Walker and Yamada (1993) observed crushing of empty shells by crabs. This indicates that accurate predation pressure cannot be estimated from broken shells in a fossil deposit.

PHYSICAL SHELL FRAGMENTATION

Driscoll (1967) was the first to study experimental shell abrasion in the field. He noted that surf action modifies bivalve shells much more slowly than laboratory abrasion in rolling barrels, which had been used up to that time to study abrasion. Abrasion starts with removing the surface sculpture; differential abrasion of various portions of the valve surface may lead to holes in the shells. Such holes (facets) were described from Wadden Sea shells, particularly *Cerastoderma*, by

Pratje (1929) and for the Dutch North Sea coast by Hollmann (1968). A continued abrasion must lead to shell fragmentation. Driscoll (1967) noted that shell fragmentation was less on sandy beaches rather than on pebbly beaches as one might expect. On sandy beaches whole valves were relatively common but few broken valves were present. This indicates that physical shell fragmentation might occur in exposed areas of the Wadden Sea, but pebbles to assist in shell breaking are scarce.

Cockle shells with abrasion holes near the umbo occur in the Wadden Sea. They can be found locally in shell concentrations high on exposed tidal flats (e.g. along the Wadden coast of Texel, and on Janssand, near Spiekeroog, German Wadden Sea, based on my own observations, September 1992). At the same locations fragments of cockle shells occur with clear marks of surface abrasion. They are not rounded but are sharp edged, and they only differ from fragments produced by predators by their surface characteristics. However, if fragments produced by predators undergo abrasion they will look very similar. This makes identification of the process which produced a particular shell fragment in a bottom sample difficult. Clear abrasion marks (surface sculpture removed, holes in shells) are rare in the Wadden Sea bottom-samples I studied for this paper, but only locally in exposed areas this process may predominate. This supports my conclusion that physical shell fragmentation is of less importance than biological fragmentation in the Wadden Sea as a whole. This observation was based on the fact that quantitative data available on predators and their consumption and fragmentation of shells can account for a large part of the fragments found in the sediment.

Linke (1939), Van Straaten (1954), and Dörjes *et al.* (1969) observed relatively high amounts of carbonates in the fine grainsize fractions of the Wadden Sea sediments. Reineck (1970, p. 32) explains this by physical destruction (abrasion) of shells. Results presented here indicate that also eider (Pl. 1, figs 4, 8; Text-figs 2–3) and probably other shell-crushing predators, produce fine carbonate particles. Shell-boring organisms will also add fine-grained carbonate particles to the sediment.

PALAEOECOLOGICAL IMPLICATIONS

Is the present the key to the past? Was shell fragmentation by predators in comparable habitats in the past as important as it is now in the Wadden Sea? Shell-breaking predators are known to have existed in the Early Cambrian. A large-scale diversification of such predators occurred in the Devonian and a large increase in families of specialized shell-breaking predators took place during the Late Cretaceous and Early Cenozoic (Vermeij 1987). Ducks are a late addition to this guild of shell-breaking predators. As for the predators described here, Anseriformes are known since the Eocene, fossil eider are only known from the Pleistocene (Uspenski 1972), but as the fossilization potential of birds is low (Schäfer 1962), they may have appeared earlier.

The present-day high intensity of shell-breaking by predators is probably characteristic for most of the Cenozoic. However, this intensity of shell fragmentation by predators was probably less before the Late Cretaceous, although the Early Palaeozoic shell fragments have been produced by predators. Palaeoecologists should be aware of the role of shell-breaking predators in producing shell fragments in marine environments. Such fragments may be of all sizes, and usually will be sharp edged, sometimes characteristic for a certain predator. In most cases they may be comparable to fragments produced by physical processes, particularly if they become abraded subsequently. 'Facets', holes in shells produced by abrasion, are the best indicators of fragmentation by physical processes, since such holes cannot be produced by predators. According to Pratje (1929) facets are related to the action of (tidal) currents confined to intertidal and shallow subtidal areas.

HIGH FIDELITY

Kidwell and Bosence (1991) suggested methods to test the fidelity of the death assemblage to the live shelly fauna. Our death assemblage data are based on weight percentages, while the data for the live shelly fauna are based on species lists and biomass data, and not for the same stations but for the entire Dutch Wadden Sea. However, live fauna data are available for a period of twenty-

five years for the tidal flats (Beukema 1976, 1981, 1982*b*, 1989) and for a shorter period in the subtidal parts of the Wadden Sea (Dekker 1989). Of Kidwell and Bosence's tests two are applicable: the percentage of dead species that are also found alive, and the comparison of the rank order of species alive and in the death assemblage (Table 3).

TABLE 3. Comparison of rank order of species in death assemblage and live shelly fauna.

Species	Intertidal biomass (Beukema 1981)		Subtidal biomass (Dekker 1989)		Overall rank living shelly fauna	Death assemblage > 2 mm	
	g afdw	(rank)	g afdw	(rank)		per cent shell weight	(rank)
Mytilus edulis	6·2	(1)	28·7	(1)	1	44·0	(2)
Cerastoderma edule	4·3	(2)	1·4	(3)	2	44·5	(1)
Mya arenaria	4·2	(3)	0·4	(5)	4	2·4	(4)
Macoma balthica	2·2	(4)	1·4	(4)	5	2·3	(5)
Hydrobia ulvae	0·2	(5)	4·9	(2)	3	< 0·1	—
Petricola pholadiformis	—	—	0·6	(6)	6	0·2	—
Ensis directus	—	—	—	—	—	0·9	(6)
Littorina littorea	—	—	—	—	—	3·5	(3)

Few species in our bottom samples were not found alive in the area. I have already referred to the Eemian *Bittium reticulatum*. Two other small gastropods, *Rissoa membranacea* and *Lacuna vincta*, found in very small numbers in some of the samples, were formerly common in the seagrass (*Zostera*) meadows (Van Benthem Jutting 1933), but disappeared after the 'wasting disease' destroyed the subtidal *Zostera* vegetation in the Wadden Sea in 1932 (Den Hartog 1987). *Ostrea edulis* also has disappeared from the Dutch Wadden Sea (Wolff and Dankers, 1981). The small bivalve *Saxicavella jeffreysi*, of which we found one valve, has never been reported alive in Dutch coastal waters (Van Benthem Jutting 1943). Thus of the twenty-six species found dead, one has disappeared since the Eemian, two since 1932, *Ostrea* this century and one has never been found alive. This results in a fidelity percentage of 80 per cent or even 92 per cent if we include data on the living fauna of the first half of this century. Kidwell and Bosence (1990, 1991) reported lower fidelity percentages (31–49 per cent) in their review of available data, when the live community was censused only once. Fidelity percentages climbed to 70–80 per cent when live census data were pooled over successive years or decades. The Wadden Sea percentage is even higher, probably because the living fauna is longer studied and poor in species. Also if we compare the rank of species we arrive at a high fidelity of the death assemblage in the live shelly fauna. For the live fauna (> 1 mm) we combined data of Beukema (1981) and Dekker (1989) to get an overall rank of species (Table 3). The first and second place in both is for *Mytilus* and *Cerastoderma*, albeit in different order, and this can partly be explained by a higher shell carbonate/biomass ratio in *Cerastoderma*. *Hydrobia*, third in the living fauna (> 1 mm) was too small to reach a high rank in the > 2 mm fraction. *Mya* and *Macoma* in both live and dead faunas occupy positions four and five. Number three in the dead fauna *Littorina* may be overestimated in the death assemblage as the samples were taken relatively close to the coast where this species occurs in higher numbers than on the tidal flats. *Ensis directus* is a recent American immigrant in the Wadden Sea. It appeared in 1979, in the German Bight (Von Cosel *et al.* 1982), and reached the Dutch Wadden Sea in 1982 (Essink 1985). It is therefore not included in the data of Beukema (1981), and Dekker (1989) dealt with pre-*Ensis directus* data (1981/82). In the 1992 samples of empty shells it already takes sixth place.

CONCLUSION

The results from this study indicate the importance of predators in shell fragmentation. This is not only be the case in shallow coastal seas where birds are the main predators in the intertidal zone. In deeper waters shell crushing by fish and crustaceans will be important. The results cast doubt on the use of a crush factor as an indicator of the degree of wear of the shell material during transport (Van Straaten 1956; Ager 1964). Correlations between fragmented shells with only water turbulence as suggested by, for example, Vokes (1948), Link (1967), Bissell and Chillinger (1967) do not seem possible. A fragmentation rate of shells to assess the autochthonous/allochthonous ratio of assemblages as suggested by Sato and Shimoyama (1992) does not take into account the role of predators. This biological fragmentation does not influence fidelity of the death assemblage to the live fauna. The high fidelity of the Wadden Sea molluscan death assemblage is encouraging for palaeoecologists. If physical abrasion had been more important, only durable skeletons would have been preserved and the fidelity to the live shelly fauna would have been low (Chave 1964). This will occur in the exposed surfzone of the open ocean, but not in the relatively sheltered Wadden Sea.

Acknowledgements. I am very grateful to Dr N. Dankers (Institute for Forestry and Nature Research, Texel) for providing me with mussel meat versus shell length data (Text-fig. 9); for critical remarks improving the typescript I thank J. J. Beukema, N. Dankers, K. W. Flessa, S. M. Kidwell, T. Piersma, C. Swennen and the two referees.

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Typescript received 13 October 1992
Revised typescript received 10 March 1993